

***TANYSTOMA DIABOLICA* NEW SPECIES  
(COLEOPTERA: CARABIDAE: PLATYNINI) FROM BAJA  
CALIFORNIA AND ITS BIOGEOGRAPHIC SIGNIFICANCE**

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*Abstract.*—*Tanystoma diabolica*, new species, is described from Baja California, and a key to the five species of *Tanystoma* is presented. A cladistic analysis of the species permits elucidation of past vicariant events leading to the present-day species. The long-time disjunction of the California fauna by vicariance at the Salinas Valley is supported by the area cladogram derived for this group.

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The genus *Tanystoma* Motschulsky comprises species found along the Pacific Coast of North America from Baja California to Oregon. Liebherr (1985) resurrected the generic name, recognizing four species. More recent studies of other genera phylogenetically close to *Tanystoma* (Liebherr, 1989) allowed assignment of an undescribed species from Baja California to *Tanystoma*. In this paper, I describe this new species, and present a cladistic analysis of the five species of *Tanystoma*. As four of the five species of *Tanystoma* are allopatric, or only narrowly parapatric, analysis of their geographic distributions in light of their cladistic relationships allows elucidation of portions of the pattern of past vicariant events leading to the present-day species.

MATERIALS AND METHODS

Specimens were examined by light microscopy using techniques of Liebherr (1985). Scanning electron micrographs (SEM) were made on gold/palladium-coated specimens using an Amray 1000 scanning electron microscope. Gold-coated body parts were mounted on points beneath the dissected specimens.

The cladistic analysis utilized the Phylogenetic Analysis Using Parsimony (PAUP) algorithm of Swofford (1985). For an initial analysis, character states were coded using out-group comparison. Where character-state polarities were ambiguous due to out-group heterogeneity, the primitive state was estimated using two criteria. Where the character transformation could be interpreted as the reduction of a complex character, Dollo's Rule of Reduction was used to establish the polarity. For other ambiguous characters, the primitive state was considered to be the more general state throughout Platynini. Two equally parsimonious cladograms were derived using these rules.

In a second analysis, characters ambiguously polarized after out-group comparison and application of Dollo's Rule were coded as missing data in the hypothetical ancestor entered in the PAUP data file. In this way, ambiguous character polarizations were free to change based on overall in-group parsimony. This analysis found one cladogram shorter than those found by the initial analysis. This shortest, and thus preferred, cladogram was used to establish likely character states in the ancestor of

*Tanystoma*, allowing a choice between *Paranchodemus* and *Rhadine* as the sister group of *Tanystoma*.

The geographic distributions of the species can be placed on the preferred cladogram to produce an area cladogram. This area cladogram is used as the basis for a scenario explaining speciation in the group. In this analysis, the widespread distribution of *T. maculicolle* is assumed to have arisen via dispersal subsequent to origin of its sympatric species. The area cladograms derived from the cladistic analysis do not include information derived from the widespread range of *T. maculicolle*.

#### CHARACTERIZATION AND AFFINITIES OF *TANYSTOMA* MOTSCHULSKY

The genus *Tanystoma* is a member of the tribe Platynini, subtribe Platyni. Species of the genus can be recognized by their pelage of sparse setae over the body surface, best observed on the basal 3 antennomeres; a mentum with anteromedial setae close together, set adjacent to the anterior marginal bead (Fig. 9); flight wings either dimorphic in the species or vestigial; and a female reproductive tract containing a short, tubular, angulate spermatheca (Fig. 14). The gonocoxae bear two lateral and one dorsal ensiform setae, (Figs. 6, 14), and 6 or 9 furrow pegs in the apical depression (Figs. 1–5). Spermathecal configuration is shared with species of *Rhadine*, prompting Liebherr (1985) to propose sister group status for the two genera.

Species of *Rhadine* differ from *Tanystoma* in the placement of the antero-medial mentum setae, which are further apart and set further from the anterior margin in *Rhadine* (Fig. 10). *Rhadine* is also characterized by the presence of only 2 furrow pegs in the apical depression of the female gonocoxae (Figs. 7, 8). If the most common number of furrow pegs observed in Platynini to date—4—is judged the primitive state, setal number has decreased during the evolution of *Rhadine* and increased in the phyletic line leading to *Tanystoma*. Several *Rhadine* species exhibit short, secondary setae on the pedicel and third antennomere, this trait best developed in the cave species (Barr, 1983; *Rhadine longicollis* Benedict, *Rhadine perlevis* Casey, *Rhadine koepkei* Barr, *Rhadine babcocki* Barr, and *Rhadine subterranea* Van Dyke of my experience). These species lack secondary setae on the scape as observed in *Tanystoma* (see Liebherr, 1985:1189, Fig. 16), suggesting that setal development on the antennae is of parallel derivation in the two groups. The rarity of these setational characters in Platynini argues against an interpretation of shared-primitive status.

Liebherr (1989) noted that the Sino-Japanese genus *Paranchodemus* Habu also exhibits an elevated gonocoxal furrow peg number of 9, a condition shared with several species of *Tanystoma*. Females of *Paranchodemus* possess short tubular spermathecae with a broad duct similar to those of *Rhadine* and *Tanystoma*. *Paranchodemus* species lack the basal pronotal seta, an absence observed in many *Rhadine*, though not *Tanystoma*. The basal 3 antennomeres of *Paranchodemus* are glabrous, unlike those of *Tanystoma*, but like those of some *Rhadine*. The anteromedial setae

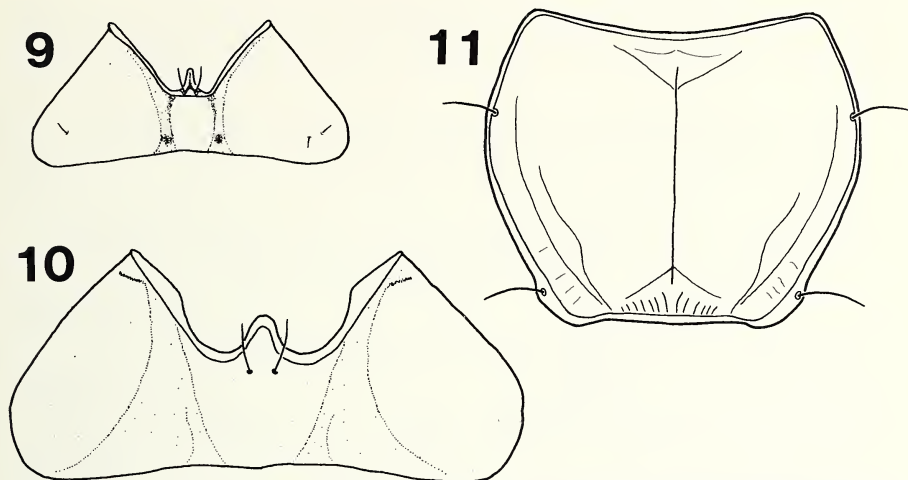
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Figs. 1–4. Apical depression of female gonocoxa, showing short furrow pegs and long nematiform setae. 1. *T. maculicolle*, with 9 furrow pegs, 3,050 $\times$ . 2. *T. cuyama*, with 6 furrow pegs, holes in membrane due to clearing of dissection, 2,561 $\times$ . 3. *T. sulcata*, with 6 furrow pegs, 3,698 $\times$ . 4. *T. striata*, with 9 furrow pegs, 2,323 $\times$ .









Figs. 9–10. Mentum ventral view. 9. *T. diabolica*. 10. *Rhadine caudata*. Fig. 11. Pronotum of *T. diabolica*, holotype.

of the *Paranchodemus* mentum are positioned as observed in *Rhadine*. Finally, the fourth metatarsus of members of all 3 genera lacks the subapical setae seen in many other platynine groups (Liebherr, 1989, Figs. 28–30). For these reasons, *Rhadine* and *Paranchodemus* were both considered potential out-groups for the initial determination of character polarities within *Tanystoma*.

In the context of Platynini possessing a short, tubular angulate spermatheca, the monophyly of *Tanystoma* is based on the following derived traits: 1) antero-medial mentum setae close together and adjacent to anterior bead; 2) basal 3 antennomeres and body surface with sparse pelage of very short setae; 3) female gonocoxae with 6 or 9 furrow pegs in the apical depression. The value of the last character awaits a full survey of this trait across more *Rhadine* species and other Platynini.

#### KEY TO ADULTS OF TANYSTOMA

This key may be used to identify the 5 species of *Tanystoma*, and supercedes that of Liebherr (1985). In that work, an unfortunate mistake in the micrometer conversion factor resulted in incorrectly reported body lengths. The correct range of body lengths is given parenthetically in the key below, that length determined as the sum of distances from: 1) apex of left mandible to cervical collar, 2) from median pronotal apex to median pronotal base, plus 3) from median pronotal base to elytral

Figs. 5–6. *T. diabolica*. 5. Apical depression of female gonocoxa, 6 furrow pegs, two nematiform setae removed, 4,376 $\times$ . 6. Left gonocoxa, ventral view, apical lateral ensiform seta broken off, 422 $\times$ . Figs. 7–8. Apical depression of female gonocoxa. 7. *Rhadine umbra* Casey, 3,218 $\times$ . 8. *Rhadine caudata* Leconte, 1,636 $\times$ .

apex. All measurements were made horizontally in the microscope field of vision with an ocular micrometer. Measurements were confirmed with a manual slide micrometer.

1. Body with lateral edges testaceous, disc of pronotum and elytra contrastingly darker, piceous to rufous ..... 2
- Body color more uniform, little contrast between disc and edges of pronotum and elytra ..... 3
- 2(1). Elytral disc with dark cloud expanded laterally to 6th stria medially, expanded to 4th stria in basal  $\frac{1}{4}$  and apical  $\frac{1}{5}$  of length, expansion from 4th to 6th stria abrupt; flight wings dimorphic, either fully developed or vestigial (length 8.2–12.6 mm) ..... *T. maculicolle* (Dejean)
- Elytral disc with central cloud evenly bordered, intervals 8 and 9 progressively more testaceous approaching lateral margin; brachypterous (length 7.8–9.8 mm) ..... *T. cuyama* Liebherr
- 3(1). Pronotum colored as the elytral disc, brunneous to piceous; brachypterous ..... 4
- Pronotum rufous, paler than the rufo-piceous head and elytra; flight wings dimorphic, either fully developed or vestigial (length 7.6–10.0 mm) ..... *T. diabolica*, n. sp.
- 4(3). Pronotum with hind margin strongly expanded posteriorly, hind angle evident, lateral margin sinuate before basal seta, notch often present in marginal bead laterad basal seta (length 9.3–11.1 mm) ..... *T. sulcata* (Dejean)
- Pronotum with hind margin moderately expanded posteriorly, hind angle rounded, lateral margin convex to straight before basal seta, marginal bead without notch near basal seta (length 7.8–11.3 mm) ..... *T. striata* (Dejean)

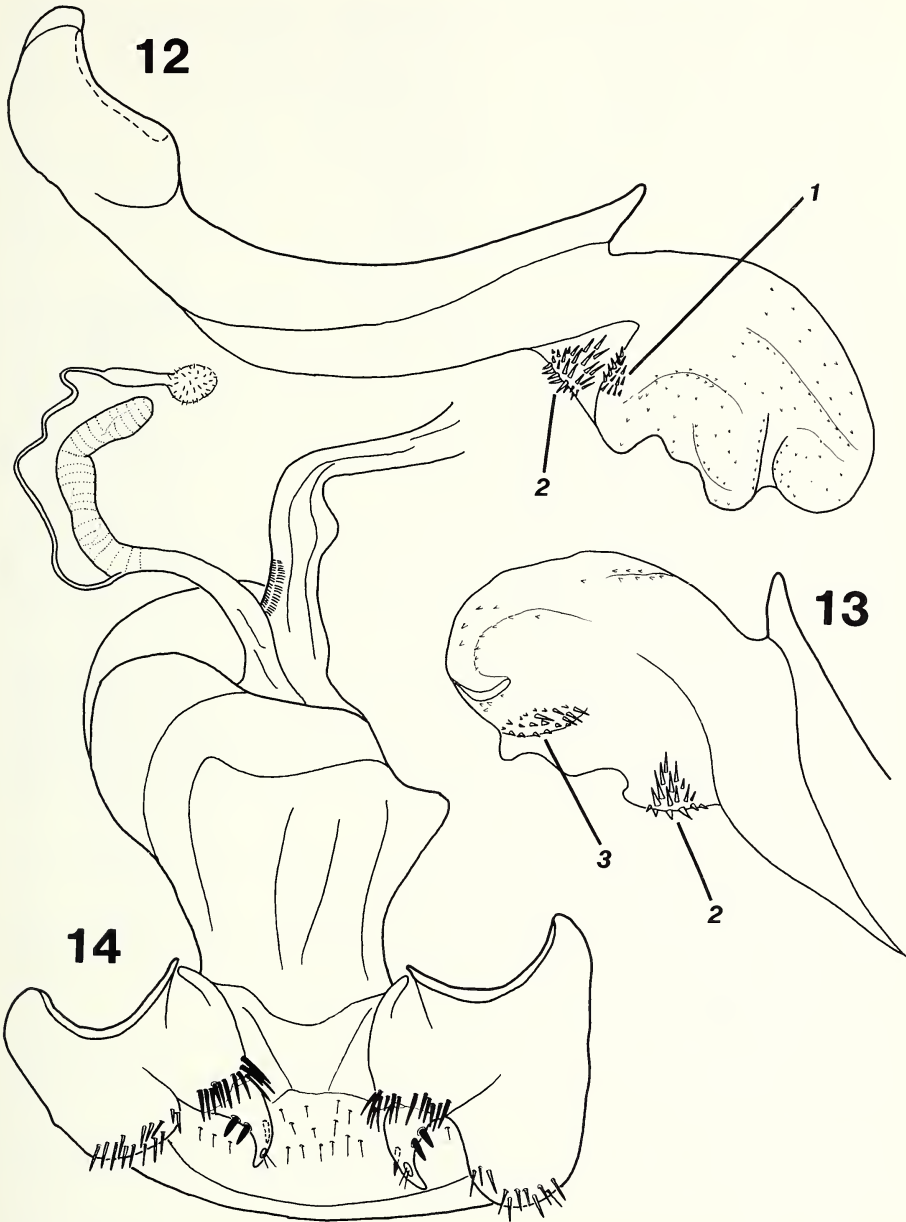
### *Tanystoma diabolica*, new species

*Diagnosis.* Head and center of elytra brunneous; pronotum, antennae, legs and elytral margins paler, rufous; pronotum narrowed basally, lateral margins sinuate, hind angles rounded (Fig. 11); flight wings dimorphic, fully developed or flap-like stubs, internal sac of male aedeagus with 3 distinct patches of spines (Figs. 12, 13).

*Description.* HEAD. Eyes moderately convex, temple expanded slightly to meet hind margin of eye; mentum with narrowly rounded well-developed median tooth (Fig. 9); foveolar pits of mentum small, shallowly sloping outside central dimple; scape, pedicel and third antennomere covered with short erect setae in addition to longer apical setae; frons and clypeus brunneous, clypeus rufo-brunneous, maxillary palps and antennal scape paler rufo-testaceous, antennal pedicel and flagellum brunneous.

PROTHORAX. Pronotum constricted basally, laterobasal margins weakly sinuate before obtuse-rounded hind angles (Fig. 11); lateral marginal depression narrow from front angle to basal  $\frac{1}{3}$  of length, gradually widening and more reflexed basally to hind seta; laterobasal depression shallow, bordered laterally by elevated margins; posterior pronotal margin convexly lobate just inside hind seta, the margin without a defined bead; median basal margin with obscure broad bead, weak longitudinal wrinkles anterad basal bead; median longitudinal impression finely engraved, meeting shallow anterior transverse impressions; anterior margin with weak bead medially, a narrow well-defined bead laterally; front angles narrowly rounded.

ELYTRA. Humeri weak even in fully-winged individuals, elytra moderately convex, sides evenly rounded, subapical sinuation weak; apex of each elytron narrowly



Figs. 12–14. *T. diabolica*. 12. Median lobe of male aedeagus, internal sac everted, dextro-ventral view, spicular fields numbered 1 and 2, holotype. 13. Apex of median lobe and sac, laevo-dorsal view, spicular fields numbered 2 and 3, holotype. 14. Female reproductive tract, ventral view.



rounded; basal groove depressed relative to disc of elytra, evenly recurved at humerus; lateral margin narrow throughout; elytral intervals slightly convex, the striae fine but continuous; 5 or occasionally 6 setae in or adjacent to the third elytral interval; 15 or 16 setae laterad eighth elytral stria; sutural interval, scutellum and elytral margins rufous, disc darker, brunneous to piceous.

**METATHORAX AND FLIGHT WINGS.** Metepisternum relatively elongate, ratio of medial length to width (c/a ratio of Liebherr, 1985, p. 1188) ranging from 1.34 to 1.50 (5 specimens); wings either with reflexed apex and fully developed (2 specimens) or reduced to vestigial flaps not extending beyond the metanotum (3 specimens).

**MICROSCULPTURE AND PELAGE.** Frons and vertex with well-developed isodiametric microsculpture, slightly stretched transversely in places; pronotal disc with regular transverse mesh microsculpture, base and laterobasal depressions with stronger, more isodiametric meshes; elytral intervals with strong isodiametric microsculpture, appearing weakly granulate; body surface covered with a pelage of sparse, small setae ranging from 0.02–0.05 mm long, these more evident on body edges and recessed areas such as the sternites posterad the metacoxae.

**MALE GENITALIA.** Median lobe of aedeagus evenly recurved, the apex short, narrowly rounded (Fig. 12); the aedeagal internal sac bearing 3 areas of stout spicules, two (positions 1 and 2) eudorsally near the base of the sac (Figs. 12, 13) and the third near the gonopore on the eudorsal side of the sac; fine, lightly sclerotized spicules covering the remainder of the sac.

**FEMALE REPRODUCTIVE TRACT.** Basal gonocoxite with apical fringe of 12–13 setae (Fig. 6); apical gonocoxite with 2 lateral and 1 dorsal ensiform setae (Figs. 6, 14); 6 furrow pegs and 2 nematiform setae in apical pit of gonocoxite (Fig. 5); bursa copulatrix short, broad, without evident microtrichia; spermatheca tubular, angulate at base and at apical  $\frac{1}{2}$ ; spermathecal gland duct entering at base of spermatheca.

**LENGTH.** 7.6–10.0 mm.

**Holotype.** Male: MEXICO: Baja California Norte: 40 mi. E El Rosario, 0.5 mi. S Hwy. 1, 4-III-1981, 1,500' elev., P. Lesica (CUIC).

**Paratypes.** MEXICO: Baja California Norte: Miller's Landing, 29-III-1973, sea level, J. Doyen and S. L. Szerlip, white light along rd. (1♂, 1♀, CISC). Baja California Sur: San Bartolome Bay, 2-VI-1925, H. H. Keifer (1♂, 1♀, CAS). Both paratypical localities are indicated in Michelbacher and Ross (1942, p. 15).

**Etymology.** This species is named both to honor my friend and botanical collector, Peter Lesica, through the latinization of his colloquial name, and for the difficulty I had in placing the species to genus.

**Distribution and Habits.** This species is known only from the Pacific Coast of central Baja California (Fig. 15B). The holotype was taken under a sleeping bag after

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Fig. 15. Distribution of *Tanystoma* species. Stippled areas on maps indicate upland pine forest. A. *T. maculicolle*. B. *T. diabolica* (area a), with localities indicated by dots; *T. cuyama* (area b); *T. striata* (areas c + d); *T. sulcata* (areas d + e).



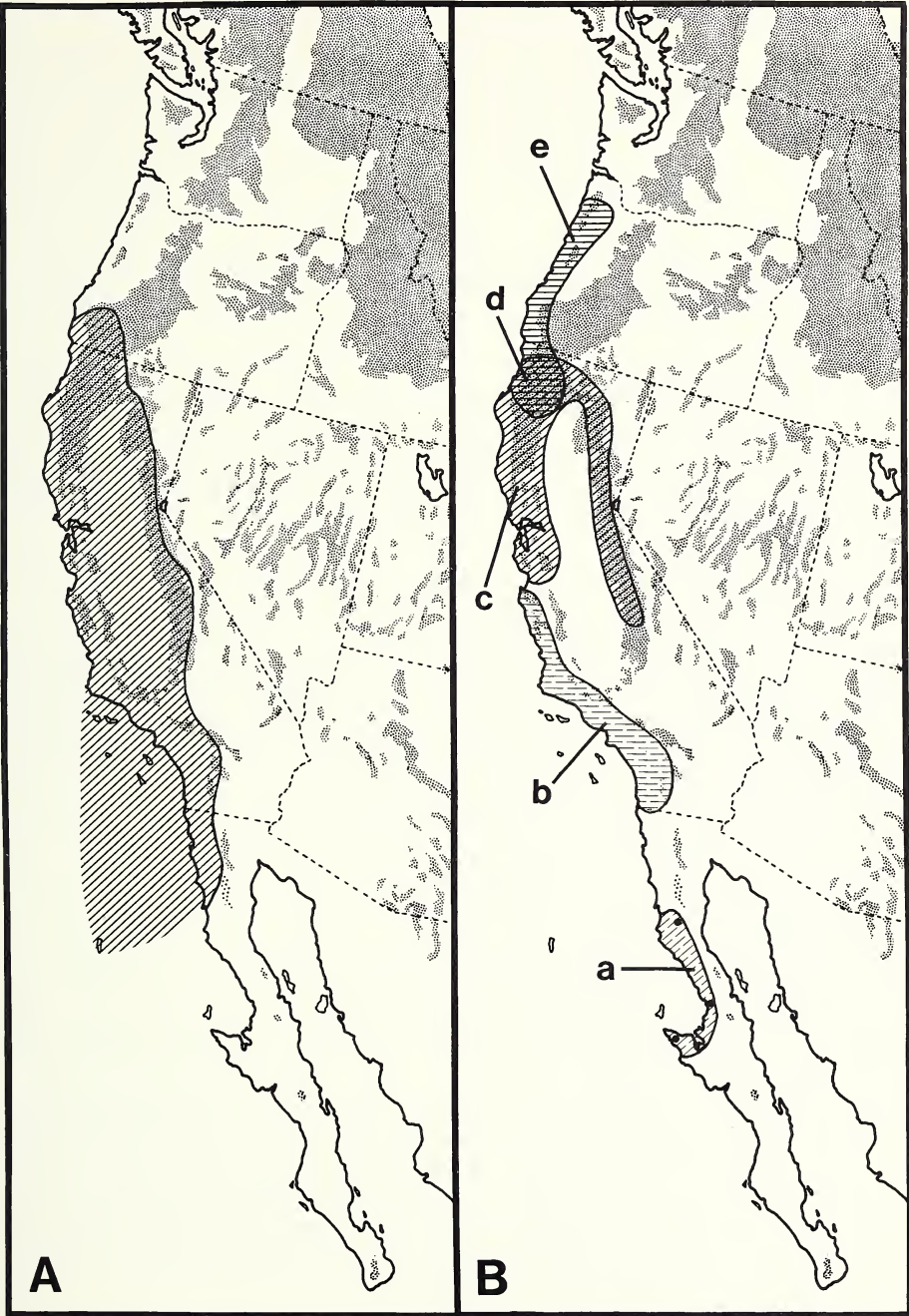


Table 1. Matrix of primitive (0) and derived (1) character states for five *Tanystoma* species.

Species	Characters									
	1*	2	3	4	5	6	7	8	9	10
<i>T. maculicolle</i>	0/1	0	0	1	0	0	0	0	1	1
<i>T. diabolica</i>	1/0	1	0	0	0	0	0	0	0	1
<i>T. cuyama</i>	1/0	1	1	1	0	1	0	0	1	1
<i>T. striata</i>	1/0	0	1	0	1	1	1	1	0	0
<i>T. sulcata</i>	1/0	0	1	0	1	1	1	1	0	0

\* Initial character values to left of slash were reversed to values at right of slash in construction of most parsimonious cladogram. Text details reasons and methods for final character-state polarization.

a nightly camp in desert habitat. Keifer (in Michelbacher and Ross, 1942) made note of "excessive aridity" at his stop at San Bartolome Bay.

The two specimens taken at light include a brachypterous female and a winged male. The San Bartolome Bay specimens also comprise a brachypterous female and a winged male. The holotype male is brachypterous.

#### CHARACTERS, CLADISTICS, AND BIOGEOGRAPHY

##### *Character Analysis*

The cladistic analysis of the five species of *Tanystoma* is based on 10 binary characters (Table 1). The initial estimates of transformation series polarity were based on out-group comparison using *Rhadine* and *Paranchodemus* and Dollo's Rule of Reduction. A description of the character states and criteria for the initial polarity decisions follow.

*Character 1.* In the primitive state the aedeagal internal sac lacks definite spinose fields, and is covered by lightly sclerotized microtrichia. In the derived state, spinose setal fields are situated on the sac. This coding is ambiguous because *Paranchodemus* have an aspinose sac, but *Rhadine* generally have one or more sclerotized fields at various positions on the sac.

*Character 2.* In the primitive state, a spinose field near the basal dorsum of the aedeagal internal sac is comprised of less than 20 spines (Fig. 12, position 2). The derived state exhibits more than 20 spines in this field. This character is unambiguously polarized because neither out-group possesses a spinose patch of configuration or position as seen in *Tanystoma*.

*Character 3.* In the primitive state, slender spines occur in the spinose field at position 2 (Fig. 12), whereas in the derived state, stout spines occur in this spicular field, as seen in *T. cuyama* (Liebherr 1985, Fig. 22). The restriction of the spicular field at position 2 to *Tanystoma* allows unambiguous coding of this character.

*Character 4.* The pronotal base is laterally sinuate in the primitive state, and convexly rounded in the derived state. Both out-groups possess cordate prothoraces, allowing unambiguous coding of this character.

*Character 5.* In the primitive state, the pronotal hind angle is rounded, either broadly rounded, or tightly rounded between nearly perpendicular basal and lateral margins (Fig. 11). In the derived state, the hind angle is more angulate. This character

is ambiguously coded as *Rhadine* may have either rounded or very sharp pronotal hind angles. *Paranchodemus* possess sharp pronotal hind angles.

*Character 6.* In the primitive state, at least some members of the species possess fully-developed flight wings. In the derived state, all members are brachypterous. Based on out-group comparison this would be ambiguously coded, as *Rhadine* are all brachypterous whereas *Paranchodemus* are winged. But, flight wing loss is considered the loss of a complex structure. Thus, this character is unambiguously polarized using Dollo's Rule of Reduction.

*Character 7.* In the primitive state, the ratio of median length to width of the metepisternum (Liebherr, 1985: 1188, c/a ratio) ranges from 1.0–1.7 within a species. The derived state is given to species in which members possess further reduced metepisterna with c/a ratios ranging from 0.94–1.12. This character coding would be ambiguously supported by out-group comparison for the same reasons as for character 6. However, just as with flight wing reduction, metepisternal reduction is considered to be an irreversible specialization.

*Character 8.* In the primitive state, the integument is colored anywhere from a pallid testaceous to rufo-brunneous. In the derived state, the cuticle is more heavily sclerotized and is rufo-brunneous to piceous in color. This character is ambiguously coded as *Rhadine* is heterogeneous, and *Paranchodemus* has a metallic-blue piceous integument.

*Character 9.* Primitively the integument is unicolorous, although appendages are usually paler than the body. In the derived state, the body dorsum is darker medially, with pallid testaceous margins. This coding is unambiguous, as all *Rhadine* and *Paranchodemus* are unicolorous.

*Character 10.* The primitive state is considered to be the possession of 3–5 dorsal elytral setae, and the derived state is the presence of more than 5 setae in at least some members of the species. This character is unambiguously coded as individuals of both *Paranchodemus* and *Rhadine* possess 5 or less dorsal setae.

### Cladistic Analysis

The cladistic analysis based on predetermined out-group polarization results in two cladograms, both of length 14 (Fig. 16A, B). In one cladogram, parallelisms are proposed for characters 2, 4, and 9 (Fig. 16A), and in the second, parallelisms are proposed for characters 2, 3, and 6 (Fig. 16B). Each cladogram includes one reversal, either character 10 (Fig. 16A) or character 1 (Fig. 16B).

These two cladograms are similar in topology to the two equally parsimonious cladograms resulting from the analysis of four *Tanystoma* species presented by Liebherr (1985). *T. diabolica* is added to this cladogram near the base, with derived states in characters 1, 2, and 10. In the prior analysis, character weighting was used to choose a preferred cladogram, that similar to topology A (Fig. 16). In this analysis an alternate, more objective procedure is made possible by the second cladistic analysis, that done with ambiguously polarized characters considered unordered. When characters 1, 5, and 8 are considered unordered, a cladogram of the topology of Figure 16B is produced, with a total length of 13. This one-step reduction is brought about by the reversed polarity in character 1. By this interpretation, a spinose aedeagal internal sac is considered the primitive state, with the aspinose sac of *T.*



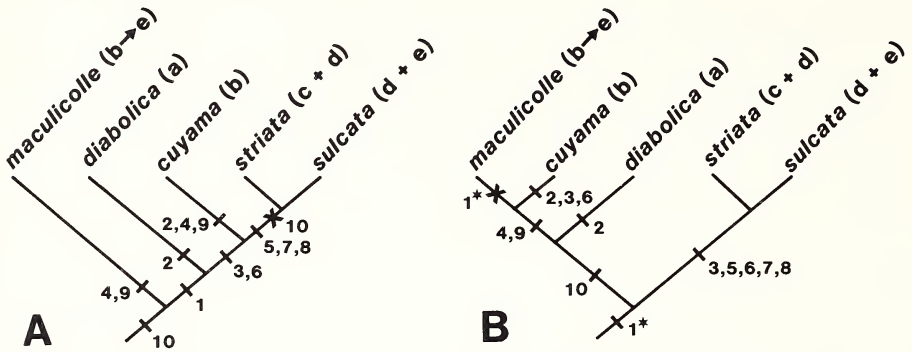


Fig. 16. Cladograms derived in the two cladistic analyses; slashes indicate character-state advances, x's indicate reversals; distributional areas of species indicated parenthetically after species name. A. Cladogram of 14 steps derived by first analysis with character polarities determined by out-group comparison. B. Second cladogram of 14 steps derived as in A, which converts to 13-step cladogram when the primitive state for character 1 is changed to maximize in-group parsimony. In 13-step cladogram, character 1 occurs once, as an advance in the stem below *T. maculicolle*.

*maculicolle* the result of derived secondary loss of spinose fields. By the criterion of parsimony, the topology of Figure 16B is thus considered the preferred topology. Its acceptance results in preference of *Rhadine* as the closest out-group to *Tanystoma*, as they share the state of a spinose aedeagal sac (character 1). *Paranchodemus* would be placed as the second closest out-group, based on a sac lacking spines, lack of pubescence on the body and basal 3 antennomeres, and a slightly different spermathecal configuration.

The acceptance of *Rhadine* as the sister group of *Tanystoma* supports the interpretation of parallel increase in gonocoxal furrow peg number in *Tanystoma* and *Paranchodemus*. If the numbers of furrow pegs in each *Tanystoma* species are overlaid onto the shortest cladogram, the basal state would be 6 furrow pegs, as observed in *T. diabolica*, *T. cuyama*, and *T. sulcata* (Figs. 2, 3, 5), with parallel increases to 9 furrow pegs in *T. maculicolle* and *T. striata* (Figs. 1, 4).

#### Biogeographic Analysis

If the two cladogram topologies of the cladistic analysis (Fig. 16A, B) are converted to area cladograms representing the areas of endemism of the four geographically restricted *Tanystoma* species, two fundamentally different cladograms result. The preferred cladogram (Fig. 16B) supports an earliest vicariant event between California north of the Salinas Valley, and the Southern Coast ranges plus portions of Baja California. In the *T. maculicolle*-*T. cuyama*-*T. diabolica* clade, vicariance between area a of coastal Baja California (Fig. 15B) and areas to the north follows the initial vicariance at the Salinas Valley. The second vicariant event within this clade separated *T. cuyama*, restricted to the southern Coast Range, from the widespread *T. maculicolle*. The divergence of *T. cuyama* can be interpreted as the speciation of peripheral populations of a proto-*T. maculicolle*. *T. maculicolle* contains populations

comprised of over 50% brachypterous individuals in the area now inhabited by *T. cuyama*, and essentially 100% brachypterous individuals on the Channel Islands (Liebherr and Hajek, 1986). During the Pliocene and Lower Pleistocene, the San Joaquin embayment connected with the Pacific Ocean via a strait at the present Santa Maria river valley, running east-west just north of Santa Barbara (Peabody and Savage, 1958). Such a barrier would have split the current range of *T. cuyama*, and may have isolated brachypterous populations of the common ancestor of *T. maculicolle* and *T. cuyama* in peripheral island habitats similar to those of today's Channel Islands. Based on the preferred cladogram, the current range of *T. maculicolle* has resulted from range expansion into at least parts of area *b* after the origin of *T. cuyama*, and into areas *c*, *d*, and *e* after the earliest vicariance within *Tanystoma* at the Salinas Valley. Colonization of the Central Valley of California by *T. maculicolle* would have occurred last, during the late Pleistocene drying of the valley floor (Wahrhaftig and Birman, 1965).

The *T. striata*-*T. sulcata* clade comprises two brachypterous species, resulting from vicariance somewhere within area *d*, with subsequent limited dispersal establishing their current area of sympatry.

Although Liebherr (1985) favored a pectinate cladogram equivalent to the current 14-step pectinate cladogram (Fig. 16A) minus *T. diabolica*, the area relationships considered representative of a general pattern in that earlier paper are represented in this study only by the preferred cladogram (Fig. 16B). The inclusion of *T. diabolica* above *T. maculicolle* on a pectinate cladogram (Fig. 16A) supports an oldest vicariant event between the Oregon + Northern to Southern California Coast Ranges, and the Sierra Columbia + Sierra Vizcaino of Baja California. The depauperate mesic-adapted fauna of Baja California limits the number of taxa likely to have sister groups including the rest of the Pacific Coast Ranges north to Oregon. But, based on past studies, sister-group vicariance between central Baja and the rest of California has not been considered a general pattern (Truxal, 1960).

In summary, preference of a taxonomic cladogram topology in this study different from the taxonomic cladogram topology preferred by Liebherr (1985), results in support for the same area cladogram, with the additional recognition of the Sierra Columbia + Sierra Vizcaino of Baja California as the sister area to the Southern Coast Range of California. The area relationships can be expressed as  $(a + b) + (c + e)$ , using the area designations of Figure 15B.

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